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# BODY LENGTH OF BONY FISHES WAS NOT A SELECTIVE FACTOR DURING THE BIGGEST MASS EXTINCTION OF ALL TIME

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**Abstract:** The Permo-Triassic mass extinction devastated life on land and in the sea, but it is not clear why some species survived and others went extinct. One explanation is that lineage loss during mass extinctions is a random process in which luck determines which species survive. Alternatively, a phylogenetic signal in extinction may indicate a selection process operating on phenotypic traits. Large body size has often emerged as an extinction risk factor in studies of modern extinction risk, but this is not so commonly the case for mass extinctions in deep time. Here, we explore the evolution of non-teleostean Actinopterygii (bony fishes) from the Devonian to the present day, and we concentrate on the Permo-Triassic mass extinction. We apply a variety of time-scaling metrics to date the phylogeny, and show that diversity peaked in the latest Permian and declined severely

during the Early Triassic. In line with previous evidence, we find the phylogenetic signal of extinction increases across the mass extinction boundary: extinction of species in the earliest Triassic is more clustered across phylogeny compared to the more randomly distributed extinction signal in the late Permian. However, body length plays no role in differential survival or extinction of taxa across the boundary. In the case of fishes, size did not determine which species survived and which went extinct, but phylogenetic signal indicates that the mass extinction was not a random field of bullets.

**Key words:** mass extinction, selectivity, macroevolution, phylogenetic comparative methods, Actinopterygii, Permo-Triassic mass extinction.

THE Permo-Triassic mass extinction (PTME) was the most devastating in the history of life. The PTME saw the extinction of 50% of families and up to 90% of species on land and in the sea (Benton & Twitchett 2003; but see Stanley 2016) and it had major evolutionary implications for modern biodiversity in determining the key clades in modern ecosystems (Sepkoski 1981). Mass extinctions have profound impacts on macroevolution: they can cause the fall of dominant groups, such as non-avian dinosaurs (Brusatte *et al.* 2014); they can release ecospace for the diversification of other clades such as mammals (Raia *et al.* 2013; Slater 2013); and they do not appear to follow the rules of normal, ‘background’ evolution (Raup 1979, 1981, 1984; Jablonski 1986, 2005; Erwin 2000). Yet the relationships between species’ traits and extinction survival is little known, and background selective processes may be absent at extinction events (Raup 1984).

Mass extinctions may operate more as a ‘field of bullets’: bad luck, not bad genes (Raup 1984; Jablonski 1986, 2005). However, there is little evidence to suggest that the loss of lineages during mass extinctions is entirely random (Raup 1984; Slowinski & Guyer 1989; Heard & Mooers 2002), and closely related taxa tend to have a similar risk of extinction (Roy *et al.* 2009; Hardy *et al.* 2012; Krug & Patzkowsky 2015).

Identifying traits that favour survival through the stresses of a mass extinction crisis has not been straightforward. It seems logical that body size, as a correlate of many other ecologically relevant traits, should correlate with extinction risk in times of mass extinction, but evidence suggests this is rarely, if ever, the case (Jablonski & Raup 1995; Smith & Jeffrey 1998; Jablonski 2005; Twitchett 2007; Friedman 2009; Harnik *et al.* 2014). The evidence linking other species- or genus-level traits to survival or extinction in the geological past has been

mixed (Jablonski & Raup 1995; Smith & Jeffrey 1998; Jablonski 2005; Twitchett 2007; Friedman 2009; Harnik *et al.* 2014). One factor often recognized as promoting increased survival is geographic range size (Jablonski 2005) but other studies contradict this (Payne & Finnegan 2007; Dunhill & Wills 2015).

In modern taxa, body size is often linked to extinction risk, with larger species having higher susceptibility than small species (McKinney 1997), in line with our current understanding of extinction risk in the modern biota (Cardillo *et al.* 2005), but this is often not the case in fossil taxa (Tomiya 2013; Smits 2015; Plotnick *et al.* 2016). For fishes, body size has been cited as an extinction risk for both ancient (McKinney 1997; Friedman 2009) and modern forms (Reynolds *et al.* 2005; Olden *et al.* 2007). Larger and smaller fish species are at threat from human activity (Reynolds *et al.* 2005; Olden *et al.* 2007) but smaller fish can respond more rapidly to changing climates and increase their chances of survival (Genner *et al.* 2010). Indeed for modern fish, extrinsic rather than intrinsic factors may be driving worldwide extinction (Duncan & Lockwood 2001).

Here we study the phylogenetic signal of extinction and selectivity of body length in non-teleostean actinopterygians during the PTME. Actinopterygians originated in the Devonian or earlier, and today are represented by the species-poor Chondrostei ('cartilage bone' fish, including the paddlefish) and Holostei (bowfin and gars), and the *c.* 30 000 species of Teleostei. Fish evolution was probably minimally affected by the PTME (Friedman & Sallan 2012) but the major clade Neopterygii (Holostei + Teleostei) survived the mass extinction, and radiated dramatically from the Middle Triassic onwards (Benton *et al.* 2013; Romano *et al.* 2014).

Our main aim here is to elucidate patterns of species loss in Actinopterygii at the PTME using a phylogenetic approach (Felsenstein 1985; Freckleton *et al.* 2002; Friedman 2009; Roy *et al.* 2009; Revell 2010; Hardy *et al.* 2012; Harnik *et al.* 2014; Soul & Friedman 2017). To test whether selection acts under the 'bad luck' or 'bad genes' models (Raup 1984; Purvis *et al.* 2000) we investigate whether lineage loss of Actinopterygii during the PTME shows evidence of phylogenetic signal. We then explore whether there is increased extinction risk related to larger body length. Using an informal composite phylogeny of actinopterygians, we explore whether there is an increased extinction risk related to larger body length.

## METHODS

### *Phylogeny*

We constructed an informal composite phylogeny of 993 species of non-teleostean Actinopterygii representing a

time range from the Devonian to the present day. The phylogeny was based upon previously published trees and taxonomy (Soul & Friedman 2015). We incorporated uncertainty in the topology by leaving unknown or uncertain relationships as polytomies. The *c.* 30 000 species of extant teleost and crown fossil members were not included in the study as they are unlikely to have been present at the PTME, and including all species was beyond the scope of our study.

We based the family-level relationships in the phylogeny on trees from Hurley *et al.* (2007), Sallan (2014), and Benton (2015). We placed genera and species in families using published phylogenies of clades within Actinopterygii. If taxa had not previously been subject to phylogenetic analyses, we used taxonomic lists to place them in appropriate clades (Soul & Friedman 2015). We applied a conservative approach to taxon placement, so the final input phylogeny was only resolved to dichotomies for 40% of nodes; these unresolved nodes represent lower taxonomic categories, mainly the uncertain relationships of genera within families. These non-dichotomous nodes were resolved to dichotomies in 1000 alternative combinations for further analysis (see below). For full details, see Puttick *et al.* (2017, supporting information).

### *Body length data*

We collected standard lengths (the length from the tip of the snout to the connection of the caudal fin to the body) for 761 taxa spanning the full timescale of analysis. Standard body lengths were used as a proxy for body size (Romano *et al.* 2014). All data were collected from published sources, and the main source of data was Romano *et al.* (2014). All body length data were log-transformed prior to analysis.

### *Dating the phylogeny*

We used species' occurrence dates to produce time-scaled phylogenies. Different tree-dating methods can affect both age estimates and subsequent macroevolutionary analyses (Halliday & Goswami 2016; Lloyd *et al.* 2016; Soul & Friedman 2017). To explore any possible biases they might have, we implemented alternative dating strategies: the 'equal' method in which nodes are dated by the first descendant's age, and zero-length branches are transformed into positive lengths by sharing edge lengths from the preceding branch (Brusatte *et al.* 2008); 'minimum branch length' ('mbl') in which nodes are again dated according to their descendant's age but branches are constrained to have a user-supplied minimum length (Bapst 2012); 'cal3' in which nodes are constrained to first

occurrences but branch lengths are sampled from distributions informed by speciation, extinction, and sampling rates of fossils (Bapst 2013); and ‘Hedman’ which is a Bayesian method for dating nodes by sampling from uniform distributions that are constrained by the ages of outgroups (Hedman 2010; Lloyd *et al.* 2016).

The ‘equal’, ‘mbl’ and ‘cal3’ methods were implemented using the function `bin_timePaleoPhy` in `paleoTree` (Bapst 2012). For the equal method the root length (vartime) was set at 5 myr; the minimum branch length was set to 2 myr with the mbl method.

We followed the approaches of Lloyd *et al.* (2016) to date phylogenies using the cal3 and Hedman methods. For the cal3 method, we restricted the tree to taxa present from the Devonian to the end-Jurassic in an attempt to estimate more realistic parameters for the model. The input parameters for cal3 (extinction and sampling rates) were estimated using the `seqTimeList` function in the R package `paleotree` (Bapst 2012). First, we sampled the range of taxon ages from the occurrence data, and these ranges were used to produce maximum likelihood estimates of extinction and sampling rates (Foote 1997). For every tree, the extinction and sampling parameters were sampled from a distribution set by these maximum likelihood estimates. As with Lloyd *et al.* (2016), we set speciation to equal extinction rate.

The Hedman method is a Bayesian approach that samples ages of nodes from a uniform distribution that is bounded by the lower age (occurrence of node-defining fossil) and an upper age (Hedman 2010). For the root, this upper age is arbitrary, but for internal nodes this is bounded by the distributions of older nodes. This method performs effectively when there is perfect congruence between node ages and phylogenetic structure. This is rarely the case as ‘outgroup’ sister taxa can be younger than descendant ‘ingroup’ taxa in real phylogenies, which is the case here. Hedman (2010) proposed a ‘conservative approach’ to ignore these situations, but this can lead to zero-length branches when applied to all branches (Lloyd *et al.* 2016). Therefore, we used the method implemented by Lloyd *et al.* (2016) that applies the conservative Hedman approach to applicable nodes, and then draws ages for the remaining node distributions bounded by these dated Hedman nodes.

As the input trees were 60% un-resolved, for each method (equal, mbl, cal3, Hedman) we produced 1000 resolved phylogenies by allowing for alternative combinations of topology in each of the time-scaled trees (Fig. 1). In terms of dating confidence, most fish taxa were resolved to the level of the stratigraphic stage, a time unit averaging 5–6 myr in duration. Some dating methods can be biased by the inclusion of living taxa (Bapst 2013), so living species were removed prior to dating the phylogenies. Implementation of the cal3 method here produced

zero-length branches (Bapst & Hopkins 2017), so for further analyses only the equal, mbl and Hedman trees were used. We visualized species diversification through time from a lineages-through-time plot generated using APE in R (Paradis *et al.* 2004).

### Macroevolutionary analysis

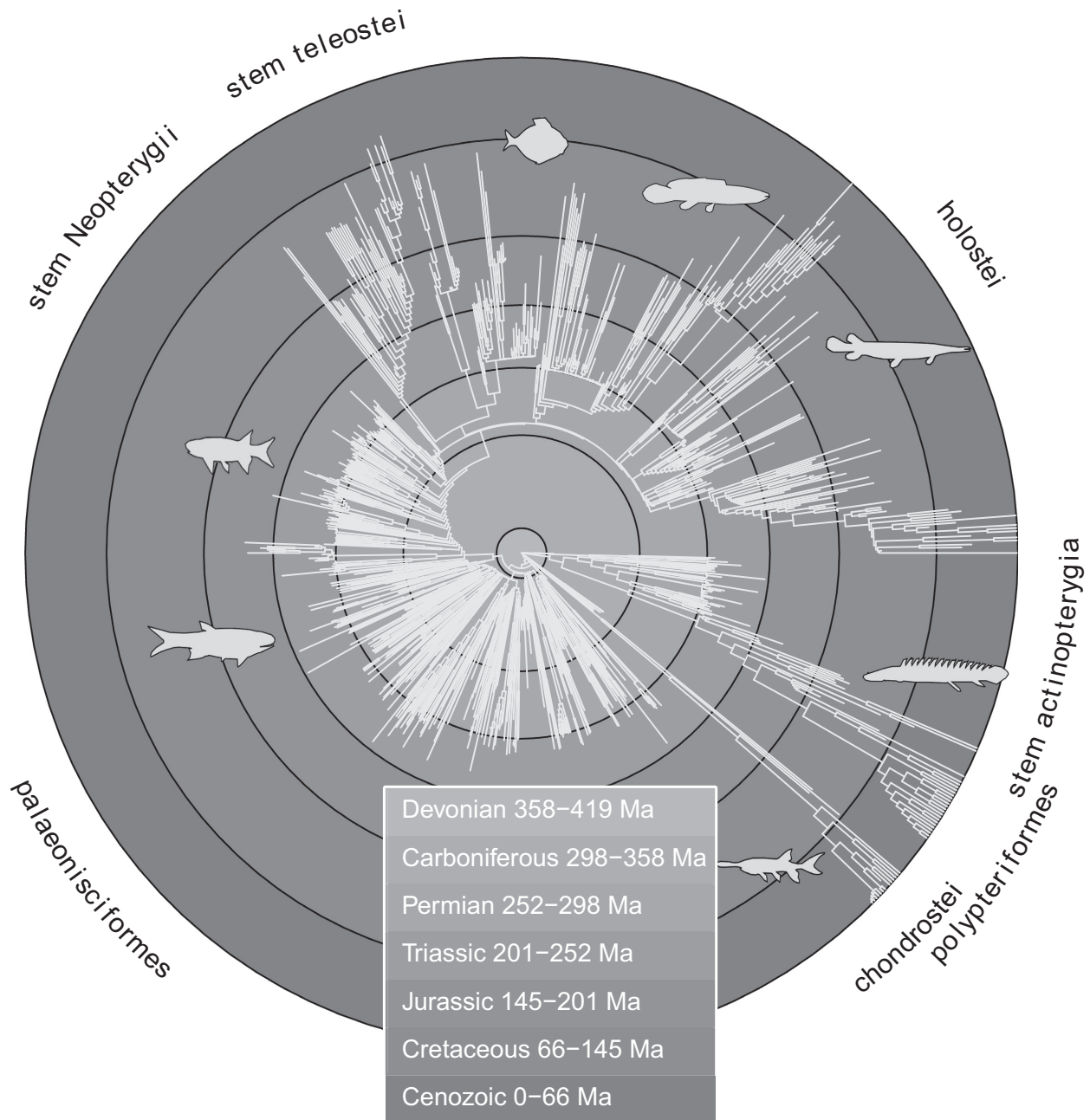
For the macroevolutionary analyses we compared species and lineages within specified time bins. In this approach, we only compared species that went extinct within a bin with lineages that were present in and survived to the end of the time bin. We excluded species that went extinct prior to the start of the time bin or arose after the end of the time bin. Bins were chosen to encapsulate named stages in the geological record or specific time frames. We analysed time bins in isolation, two from the late Permian (Lopingian, Changhsingian) and three from the Early Triassic (first 0.5 myr of Triassic, Induan, Olenekian), as well as bins from multiple time frames across the boundary (Changhsingian–Induan, and Changhsingian–Induan–Olenekian) and into the Early Triassic (Induan–Olenekian, Early Triassic).

In this approach, the tree was pruned to lineages present in a bin; the tips were kept with their original values (i.e. body length) but for lineages that spanned the boundary we used either ancestral node or tip values depending on which was nearest to the boundary. In phylogenies with fossils, the accuracy of node reconstructions is increased (Puttick & Thomas 2015; Puttick 2016) so there is increased confidence in employing reconstructed node values, rather than remote tip values.

The majority of analyses were conducted in the software platform R (R Core Team 2016) using published packages or custom-written code (Puttick *et al.* 2017).

### Clustered vs random extinction

We tested whether the victims were phylogenetically clustered, or whether loss of lineages was random with regard to phylogeny during the PTME (Raup 1984; Roy *et al.* 2009; Hardy *et al.* 2012; Soul & Friedman 2017). The extent to which extinction was phylogenetically conserved or random was tested using the *D* statistic (Fritz & Purvis 2010), which is an estimate of phylogenetic signal in binary traits. Analyses of the *D* statistic were conducted in the R package `caper` (Orme 2012). The *D* statistic is calculated by estimating the mean of observed trait differences in sister clades across the tree for tips and node values estimated with independent contrasts (Felsenstein 1985). The observed value of sister comparisons is scaled by generating two simulated scenarios of trait evolution,



**FIG. 1.** One of the time-scaled phylogenies from the equal method of all taxa included in the study from the Devonian to the present.

representing models of phylogenetic clustering and random dispersal respectively. The model of phylogenetic signal is generated by analysing data that are simulated under a Brownian motion (BM) threshold model, and a random dispersal value is modelled by shuffling trait values at the tips (Fritz & Purvis 2010). These permutations were performed 1000 times for each analysis. By scaling the observed value to these two simulated values,  $D$  may be compared across phylogenies and datasets: a  $D$  statistic value of 1 signifies random trait evolution; 0 is a

Brownian motion signal. Values of  $D$  can fall outside this range if trait data are overly clumped ( $D > 1$ ) or overly dispersed ( $D < 0$ ). All of our data satisfied the criteria for acceptable levels of estimation accuracy for the  $D$  statistic regardless of the phylogenetic structure or extinction prevalence: every tree was fully resolved and contained more than 50 tips (Fritz & Purvis 2010).

Alternative measures of the phylogenetic signal of extinction have been employed in studies of the fossil record (Roy *et al.* 2009; Hardy *et al.* 2012; Soul &



Friedman 2017). For example, Moran's  $I$  in a phylogenetic context (Gittleman & Kot 1990) to estimate the strength of extinction clustering (Hardy *et al.* 2012; Soul & Friedman 2017). Briefly, Moran's  $I$  calculates the autocorrelation between variables (here binary traits) that are weighted for each observation by the inverse of their cophenetic distance (Gittleman & Kot 1990; Paradis 2017). The null value of  $I$  is dataset-dependent but observed values that are non-significantly different from  $I$  are interpreted as indicating a BM process, lower values of  $I$  signify random clustering and higher values of  $I$  show high levels of clustering. Here we compared the results of the  $D$  statistic with Moran's  $I$  (Hardy *et al.* 2012; Soul & Friedman 2017), but we favour the use of the  $D$  statistic as it is well suited for extinction clustering analyses (Hardy *et al.* 2012; Münkemüller *et al.* 2012).

### Selectivity of body length

Data at the tips of phylogenies are not statistically independent, so phylogenetic history has to be accounted for in the analyses (Felsenstein 1985). In order to do this, we used a phylogenetic generalized least squares (PGLS) model in the R package caper (Orme 2012) with one explanatory variable (two states: extinct, not extinct) and the response (body length). We estimated the effect of phylogenetic history using the parameter  $\lambda$  (Pagel 1999) concurrently with model parameters (Freckleton *et al.* 2002). The value of  $\lambda$  can vary between 0, in which traits evolve independently of phylogeny, and 1, in which trait evolution follows the expected value under a Brownian motion model (Pagel 1999; Freckleton *et al.* 2002).

Ancestral length estimation was done using the model StableTraits (Elliot & Mooers 2014). StableTraits relaxes the assumptions of BM by sampling rates from a heavy-tailed, rather than normal distribution, and thus incorporates rate variation into ancestral size estimation. This approach has allowed StableTraits to be more accurate than BM in reconstructing ancestral states. The model was run over two independent chains for 400 000 generations and the first 10% were discarded as 'burn-in'. Chain convergence was judged by potential scale reduction factor  $<1.1$ . The relative fit of the StableTraits model was superior to BM across all datasets and trees (median  $\Delta$  Bayesian Predictive Information Criterion  $> 147$  across all 3000 trees).

## RESULTS

### Diversity through time

There was a catastrophic decline in species numbers during the PTME that extended into the earliest Triassic

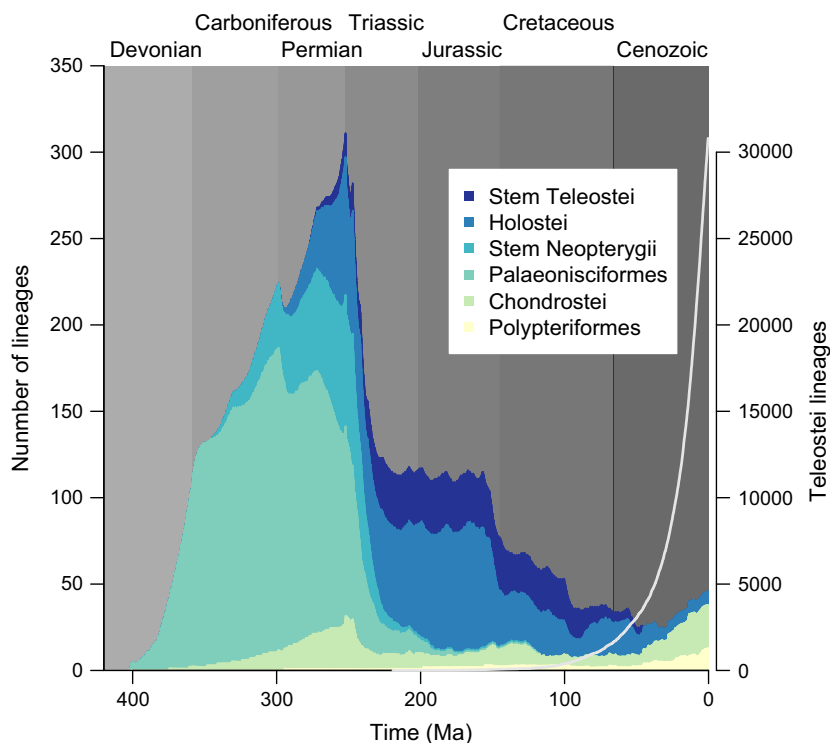
(Figs 1, 2). All groups suffered drops in diversity, but this was most evident in the diversity of previously dominant groups, such as the Palaeonisciformes. Rates of lineage disappearance were higher in the earliest Triassic than the late Permian (Table 1).

### Non-random extinction

Analysis using the  $D$  statistic resulted in the same general patterns in clustering, regardless of the method used to date the phylogenies: low clustering in the late Permian, and higher phylogenetic signal in the Early Triassic (Table 1; Fig. 3). Across all trees, there is a decrease in the  $D$  statistic to zero (indicating phylogenetic signal) in the earliest Triassic (Induan and early Olenekian bins) compared to the late Permian. There is strong support for a random signal in the Changhsingian at the end of the Permian (only 0.5–20.7% analyses differ from random across all dating strategies). Generally there is evidence of stronger clustering in the Early Triassic. However, the 0.5 myr and Olenekian time bins show the opposite pattern, as  $D$  statistics indicate a more random signal of extinction (Table 1). Across all tree-dating strategies, the late Permian (Lopingian) shows a more random pattern of extinction compared to the Early Triassic (Induan, early Olenekian).

General trends in phylogenetic signal shown by the  $D$  statistic are comparable across tree dating strategies, but they do show some differences. Values of  $D$  are lowest in the Hedman phylogenies, intermediate in the equal phylogenies and largest in the mbl phylogenies (Table 1). The Hedman phylogenies indicate a high phylogenetic signal in the Early Triassic, as three time bins (Induan, Induan–Olenekian, early to mid Triassic) all show 100% for a BM model. However, values of  $D$  are higher in the same bins analysed with the equal and mbl phylogenies, and these trees also show weaker support for BM (69–100% of trees reject BM across comparable bins). Furthermore, the uncertainty and absolute value of the  $D$  statistic is much higher in the equal and mbl phylogenies compared to the Hedman trees (Fig. 3). The significance of extinction clustering in the latest Permian (Changhsingian) is similar across all dating strategies, as they indicate only a subset of phylogenies can reject a random signal (0.4–20.7% across dating strategies). In the Early Triassic, there is greater evidence that the random signal can be rejected ( $>92\%$  in all time bins).

The patterns shown by Moran's  $I$  are largely congruent with those shown using the  $D$  statistic (Table 1). For example, there is a negative correlation (albeit largely non-significant) in the Changhsingian, indicative of random extinction, which is the same pattern shown by the  $D$  statistic in this bin. In all dating strategies, this switches



**FIG. 2.** Cumulative lineages-through-time plot showing the diversity of different clades of actinopterygians through time. Note the massive dip at the PTME (c. 252 Ma), but importantly that this did not mark the end of the major groups ‘Palaeonisciformes’ and stem Neopterygii, which declined through the Triassic and Jurassic. Lineage numbers do not recover to pre-extinction levels here, because of the omission of the neopterygian clade Teleostei. The approximate rise of extant teleosts (grey line) indicates they were unaffected by the PTME, and their dominance arose much later. Colour online.

in the Early Triassic to a positive correlation, showing higher evidence for phylogenetic signal in traits.

### Selectivity

There is little evidence that body size was linked to survival during the PTME (Table 2). There is a significant difference between extinct and surviving lineages across only 16.9% of the analyses, representing alternative phylogenies and all time bins. There is no significant support for a difference in body length between extinct and surviving lineages (Table 2). The explanatory power of the analyses (as judged by the adjusted  $R^2$ ) is generally low (median = 0.0039) as there is a large variance in body lengths in surviving and extinct lineages (Fig. 4).

Previous analyses have noted that body size selectivity can be hidden, as taxa from ‘dead clade walking’ groups survive, only to die out soon afterwards (Sallan & Galimberti 2015). These clades may have high or small body sizes, and this would prevent a signal of selectivity being detected, particularly as many genera of fishes that survived the PTME were long-lived (Romano *et al.* 2014). Therefore, we re-analysed selectivity but classified survival in a different way. In the first analysis, taxa were marked as surviving if they did not go extinct in the bin, but in this second analysis lineages were only classified as survivors if they gave rise to at least ten descendant species.

The results of this analysis are similar to the original analysis, and actually indicate a smaller difference in body size between surviving and extinct lineages (Fig. 5).

The median body lengths of species that went extinct in the Changhsingian are generally higher than those of surviving species (Fig. 4), but this trend is not statistically significant in the vast majority of cases (Table 2). Additionally, this trend disappears when only taxa ancestral to at least ten species are considered as surviving (Fig. 5).

In a non-phylogenetic analysis, there was no significant difference in body size of taxa going extinct between stages through the PTME (0.5 myr, Induan, Induan–Olenekian; Fig. 6). There is no significant difference in sizes of taxa that go extinct within these three time bins (Kruskal–Wallis test,  $df = 2$ ,  $p = 0.95$ ). Generally, in studies such as these, phylogenetic comparative methods should be used (Freckleton 2009), but here the comparison with a non-phylogenetic result allows us to test whether the phylogenetic results from an unresolved phylogeny are too conservative (Abouheif 1998).

## DISCUSSION

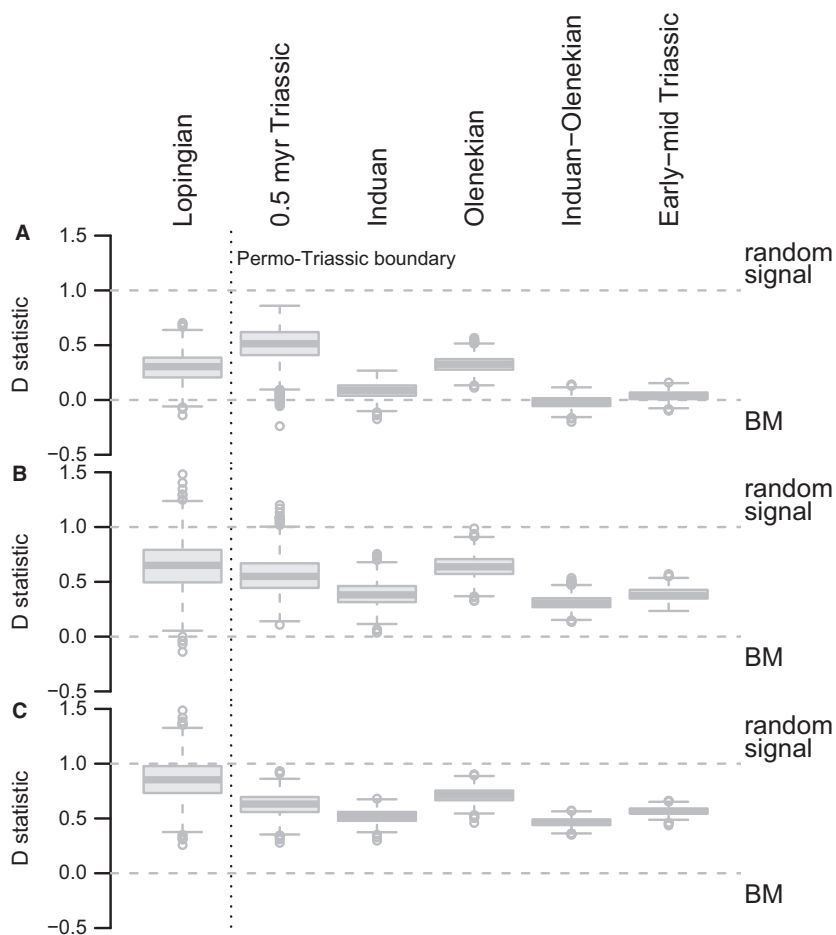
Body length appears to have played no role in the extinction or survival of non-teleostean actinopterygian fishes through the PTME, even though the total diversity of non-teleostean actinopterygians was dramatically reduced

**TABLE 1.** Summary of the phylogenetic signal of extinction in bins before and after the Permo-Triassic mass extinction.

	<i>D</i> statistic				Moran's <i>I</i>	
	Number of lineages present in bin	Lineages extinct in bin (%)	<i>D</i> statistic	Percentage significant different to random	Percentage significant different to BM	Moran's <i>I</i>
Hedman	Lopingian	5.04–7.61	0.304 (0.0205, 0.542)	100	16.3	0.0055 (0.003, 0.008)
	Changhsingian	0.426–2.24	0.949 (0.09, 2)	20.7	32.4	–0.001 (–0.004, 3e–04)
	0.5 myr Triassic	4.94–7.24	0.513 (0.09, 0.7)	97.8	69.7	0.01 (9e–05, 0.02)
	Induan	10.7–12.5	0.0848 (–0.05, 0.2)	100	0	0.02 (0.009, 0.03)
	Induan–Olenekian	22.2–24.7	–0.0155 (–0.1, 0.08)	100	0	0.02 (0.02, 0.03)
	Olenekian	13–15.1	0.326 (0.1, 0.4)	100	57.4	0.006 (0.003, 0.01)
	Early–mid Triassic	59–63.2	0.0385 (–0.05, 0.1)	100	0	0.03 (0.02, 0.04)
	Lopingian	3.04–8.44	0.65 (0.2, 1.0)	67.4	67.8	0.016 (0.002, 0.03)
	Changhsingian	0.279–1.91	2.39 (0.5, 1)	0.4	46.7	–0.005 (–0.007, –0.004)
	0.5 myr Triassic	7.87–15.6	0.55 (0.2, 0.9)	92.6	87.6	0.1 (0.02, 0.2)
Equal	Induan	14.1–19.4	0.381 (0.1, 0.6)	100	69.9	0.1 (0.06, 0.2)
	Induan–Olenekian	26.8–31.7	0.306 (0.1, 0.4)	100	84.7	0.1 (0.08, 0.2)
	Olenekian	14.7–20.1	0.637 (0.4, 0.8)	98.3	99.7	0.05 (0.02, 0.09)
	Early–mid Triassic	64.7–69.9	0.376 (0.3, 0.5)	100	100	0.07 (0.05, 0.09)
	Lopingian	3.3–8.88	0.853 (0.4–1.2)	41.8	97.2	0.3 (0.007, 0.06)
	Changhsingian	0.326–2.31	2.61 (–0.1, 39.6)	0.5	60.4	–0.007 (–0.009, –0.005)
	Half Ma	10.2–18.3	0.632 (0.4, 0.8)	99.5	99.7	0.07 (0.04, 0.1)
	Induan	16.2–21.4	0.52 (0.4, 0.6)	100	99.9	0.09 (0.08, 0.1)
	Induan–Olenekian	28.6–32.1	0.465 (0.3, 0.5)	100	100	0.09 (0.09, 0.1)
	Olenekian	15.7–20.2	0.712 (0.5, 0.8)	99.7	100	0.05 (0.04, 0.06)
mbl	Early–mid Triassic	68.1–72.2	0.567 (0.5, 0.6)	100	100	0.06 (0.04, 0.08)
	Lopingian	5.04–7.61	0.304 (0.0205, 0.542)	100	16.3	0.0055 (0.003, 0.008)
	Changhsingian	0.426–2.24	0.949 (0.09, 2)	20.7	32.4	–0.001 (–0.004, 3e–04)
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	Changhsingian	0.279–1.91	2.39 (0.5, 1)	0.4	46.7	–0.005 (–0.007, –0.004)

All values are summarized across analyses based on 1000 trees dating use each method (Hedman, equal, mbl respectively). The number of lineages present in the bin is variable as the age of taxa are stochastically sampled from a uniform distribution. For the *D* statistic and Moran's *I* the median value is shown as well as the 95% confidence interval. For the *D*, the values summarize the percentage of phylogenies that significantly differ from a random or BM model. For Moran's *I* a negative correlation signifies a random signal, and positive correlation shows evidence of phylogenetic clustering.





**FIG. 3.** Boxplots of the  $D$  statistic through time in different time bins for the phylogenies dated using the: A, Hedman; B, equal; C, mbl methods. A  $D$  value of 1 would indicate random extinction and 0 would show clustering. Generally, clustering increases during the Triassic following the mass extinction compared to the late Permian (Lopingian). However, the first 0.5 myr of the Triassic and Olenekian time bins indicate values of  $D$  that are similar or slightly lower (B, C), or increased (A) compared to the Triassic. Across all tree dating methods there is more evidence of increased clustering after the extinction (Induan) and throughout the entire Early Triassic compared to the Lopingian.

by the mass extinction. However, there is a higher phylogenetic signal in extinction in the earliest Triassic compared to that of the late Permian.

#### *Phylogenetic signal of extinction*

In the Early Triassic, extinction was not random with regard to phylogeny, assuming a model of Brownian motion (Raup 1984; Slowinski & Guyer 1989; Heard & Mooers 2002). This suggests that there may be traits other than body length that play a role in extinction selectivity (Green *et al.* 2011). In the period preceding the PTME, extinction was random, particularly in the Changhsingian, but in the extinction aftermath species loss shows a higher phylogenetic signal (Fig. 3). Similar patterns have been observed for other clades in the fossil record, such as Ordovician brachiopods (Krug & Patzkowsky 2015). However, in some clades, the phylogenetic signal of extinction decreases across the boundary, such as bivalves across the K-Pg (Roy *et al.* 2009), and tetrapods through the PTME (Soul & Friedman 2017). There is less phylogenetic signal in extinction following the boundary here

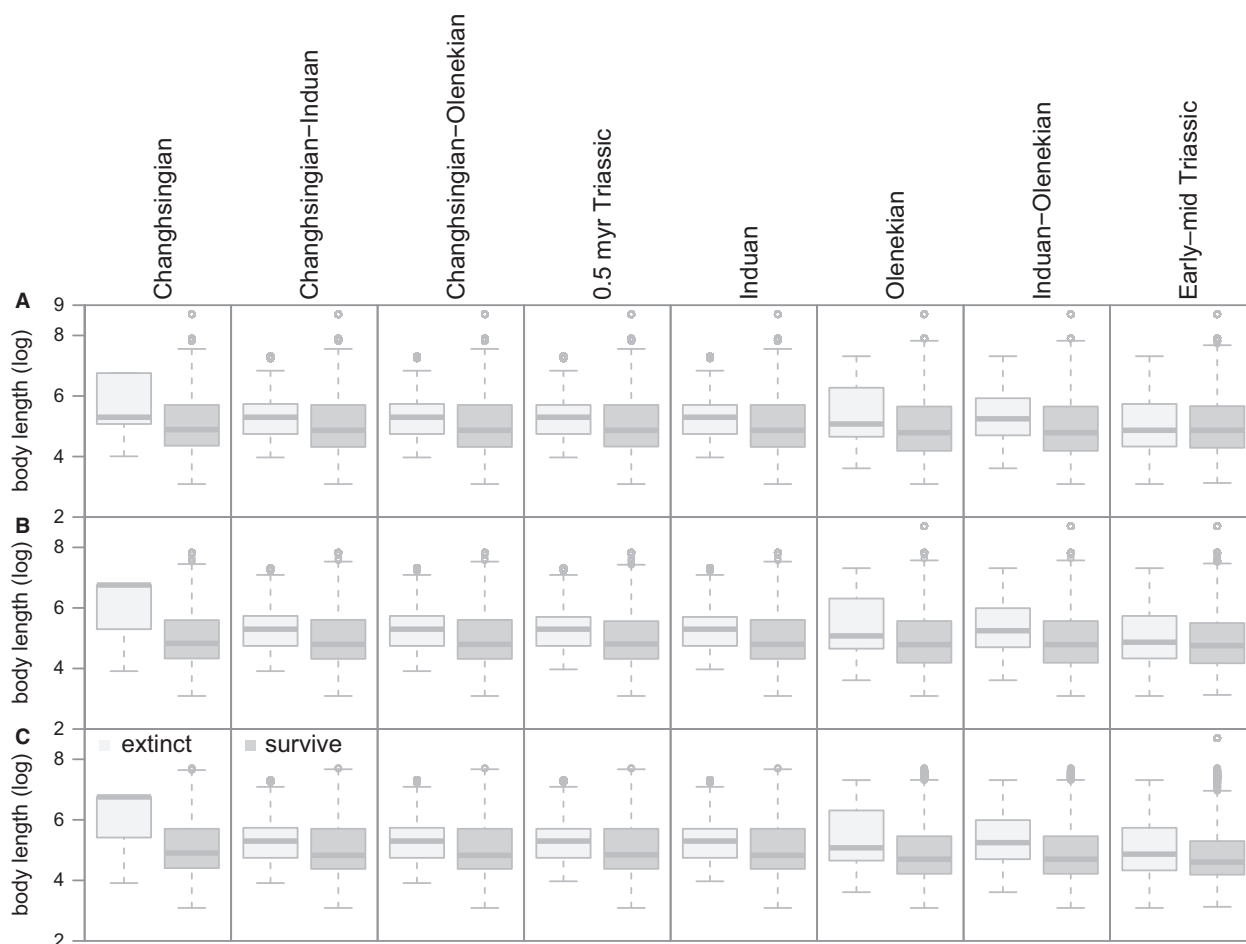
in two specific bins (0.5 myr following extinction, Olenekian) but the opposite pattern is seen when considering the Early Triassic as a whole (Fig. 3). Overall, there is general support for an increase in clustering during the most intense period of extinction during the PTME (Table 2). Thus a possible explanation for the increase in clustering following the boundary is that this is the time of the highest rates of lineage loss, but the correlation between rates of lineage loss and extinction selectivity is not always significant (Roy *et al.* 2009). Another possibility is that clustered origination in the early Triassic could cause an identical effect to clustered extinction.

Measurements of phylogenetic signal can be biased by sampling and tree dating methods (Hardy *et al.* 2012; Soul & Friedman 2017). Changes in fossil sampling rates and the implementation of alternative dating metrics can cause differences in phylogenetic clustering (Soul & Friedman 2017). Low levels of sampling, biogeography, and the method of branch scaling can cause an estimate of higher clustering (Krug & Patzkowsky 2015; Soul & Friedman 2017). We do not consider biogeography in our analyses, but the global scale of our study means it is unlikely that extinctions of fishes through the PTME were local or regional.

**TABLE 2.** The percentage of phylogenies that show significant differences between body lengths of surviving lineages and taxa going extinct in different time bins.

		Percentage significant different body length for survivors and extinct lineages	$\lambda$	Adjusted $R^2$	Percentage significant different body length for survivors (ancestral to at least 10 species) and extinct lineages
Hedman	Changhsingian	0	0.71 (0.625, 0.822)	-0.00199 (-0.00253, 0.0013)	12.6
	Changhsingian-Induan	2.4	0.708 (0.627, 0.795)	0.00107 (-0.00197, 0.00623)	14.3
	Changhsingian-Induan-Olenekian	24.9	0.698 (0.614, 0.777)	0.00486 (-0.00169, 0.0111)	71.0
	0.5 myr Triassic	3.4	0.712 (0.625, 0.82)	-0.00114 (-0.00254, 0.00754)	14.7
	Induan	0.9	0.709 (0.628, 0.797)	0.000946 (-0.00179, 0.0058)	14.3
	Olenekian	0.8	0.709 (0.626, 0.791)	0.00069 (-0.00209, 0.0057)	65.0
	Induan-Olenekian	24.4	0.699 (0.616, 0.78)	0.00479 (0.000608, 0.0111)	71.0
	Early-mid Triassic	98.1	0.722 (0.647, 0.794)	0.0154 (0.00764, 0.0249)	15.0
	Changhsingian	0.8	0.786 (0.685, 0.863)	-0.00229 (-0.00371, 0.00424)	21.3
	Changhsingian-Induan	19.3	0.758 (0.67, 0.839)	0.00426 (-0.00249, 0.0157)	10.5
Equal	Changhsingian-Induan	81.2	0.741 (0.664, 0.817)	0.0129 (-0.000801, 0.0241)	10.7
	Changhsingian-Induan-Olenekian	11.5	0.767 (0.676, 0.848)	0.00122 (-0.00331, 0.017)	11.4
	0.5 myr Triassic	14.2	0.759 (0.67, 0.839)	0.00373 (-0.00265, 0.015)	10.4
	Induan	22.7	0.761 (0.677, 0.845)	0.00578 (-0.00211, 0.0168)	18.2
	Olenekian	81.9	0.742 (0.665, 0.817)	0.0125 (-0.000544, 0.0231)	10.7
	Induan-Olenekian	60.7	0.721 (0.655, 0.801)	0.008 (-0.00208, 0.0159)	77.0
	Early-mid Triassic	16.0	0.751 (0.66, 0.829)	-0.00191 (-0.0038, 0.00816)	15.0
	Changhsingian	16.9	0.734 (0.655, 0.814)	0.0041 (-0.00231, 0.0164)	12.0
	Changhsingian-Induan	82.8	0.76 (0.682, 0.827)	0.0169 (-0.00192, 0.0296)	16.0
	Changhsingian-Induan-Olenekian	9.9	0.743 (0.654, 0.819)	0.000439 (-0.00371, 0.0186)	15.0
mbl	0.5 myr Triassic	11.4	0.734 (0.655, 0.813)	0.00307 (-0.00273, 0.0154)	12.0
	Induan	42.8	0.789 (0.713, 0.859)	0.00915 (-0.00282, 0.0218)	17.0
	Olenekian	85.6	0.761 (0.684, 0.827)	0.0161 (-0.00191, 0.0284)	16.0
	Induan-Olenekian	22.8	0.723 (0.65, 0.816)	0.00429 (-0.00237, 0.012)	18.6
	Early-mid Triassic				

The phylogenetic signal ( $\lambda$ ) of the PGLS models and adjusted  $R^2$  value are also summarized. The same pattern of no significant difference between the body size of surviving and extinct lineages is also seen when survivors are classed as lineages that give rise to at least ten descendant species.

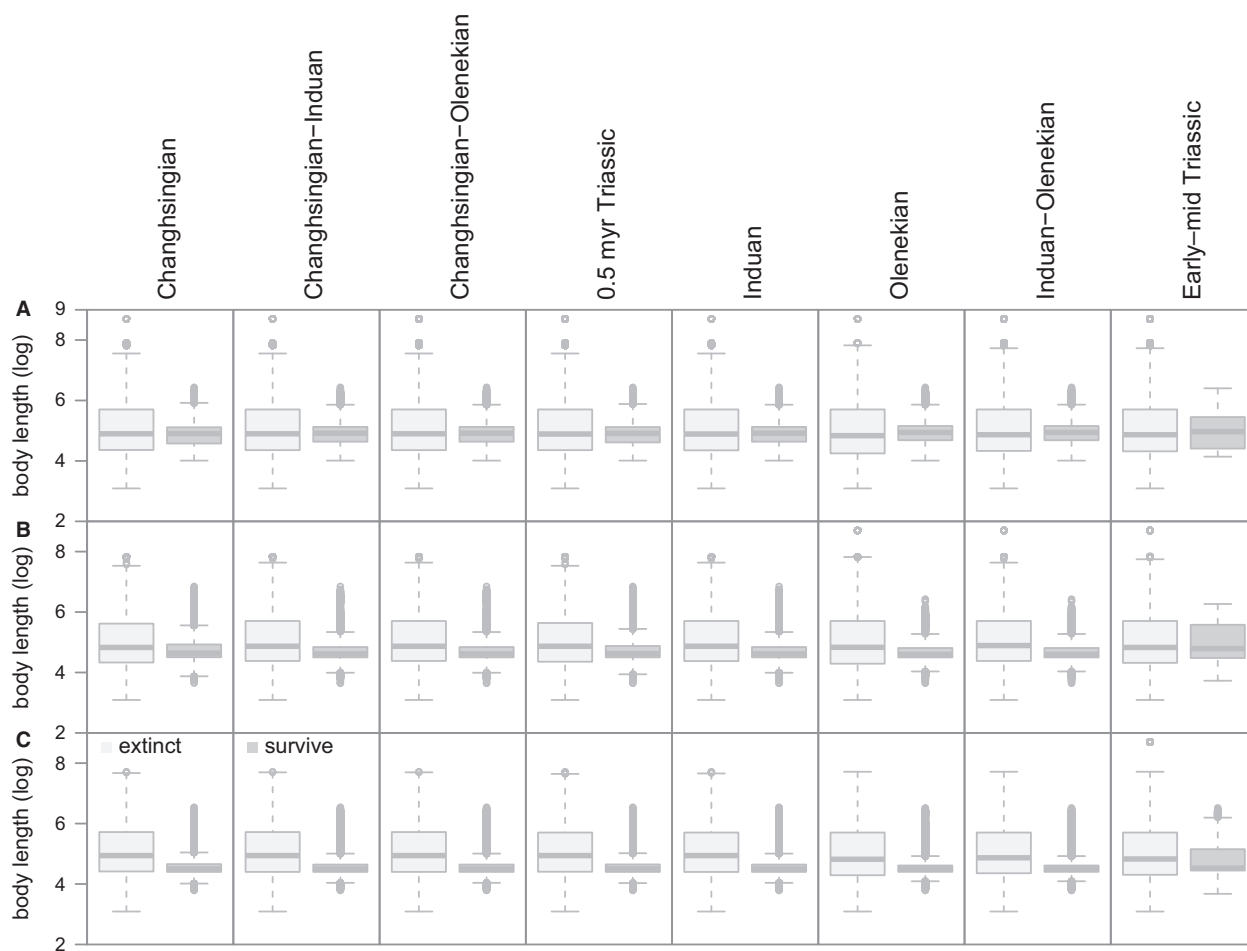


**FIG. 4.** Boxplots summarizing the body lengths of taxa that went extinct (light grey) compared to those that survived (dark grey) in different time bins from the late Permian to Early Triassic for phylogenies dated using the: A, Hedman; B, equal; C, mbl methods. For these analyses, the phylogenies were pruned to lineages and tips present in the time bin. Taxa were classified as extinct if they disappeared during the interval, and as surviving if they were present at the end of the time bin. Generally across all time bins and tree dating strategies, there is no significance between the body lengths of surviving and extinct lineages analysed using phylogenetic generalized least squares models.

Here we attempt to avoid all these biases by sampling as densely as possible from before and after the extinction interval, using non-named time bins (e.g. the first 0.5 myr of the Triassic), and repeating calculations over all variants of trees to represent phylogenetic uncertainty. We iterate over 3000 phylogenies with alternative branching patterns and times of occurrences, and with these data we obtain the same trends in the patterns of extinction clustering across alternative tree-dating metrics (Table 1). Because many taxa exist only from one named time bin, it is also possible that a false signal of higher clustering in the Early Triassic could be the result of Lagerstätten occurrences, but sampling density in the Permian has recently improved (Romano *et al.* 2014) increasing the support for a true signal of random lineage loss at this time. We found that the Hedman trees resulted in higher (less clustered) estimates of the  $D$

statistic compared to the equal or mbl trees (Soul & Friedman 2017). There is higher uncertainty in the mbl and equal trees, as is shown by the high variance of the  $D$  statistic in the Changhsingian, but this is likely to arise from the low proportion of extinction within this time bin (Table 1). Despite these differences in the absolute values, the patterns of extinction clustering are similar across all dating strategies.

The informal method of tree construction that we employed might also introduce a bias. For the analyses of trait evolution and clustering of extinction, this could damp the phylogenetic signal and produce type II statistical errors (Abouheif 1998; Rabosky 2015). However, informal methods to construct palaeontological phylogenies perform well in macroevolutionary analysis (Soul & Friedman 2015) and the use of taxonomy and phylogenetic knowledge means they are far from random.



**FIG. 5.** Summary of body lengths for taxa that went extinct (light grey) compared to those that survived and gave rise to at least ten descendant species (dark grey) in different time bins from the late Permian to Early Triassic for phylogenies dated using the: A, Hedman; B, equal; C, mbl methods. As many taxa can survive a mass extinction but succumb to extinction soon afterwards, the aim of this analysis was to clarify whether body lengths differed between extinct taxa and successful surviving lineages (i.e. those that were ancestor to at least ten descendants). There is some signal in these analyses that particularly large or small species were more susceptible to extinction.

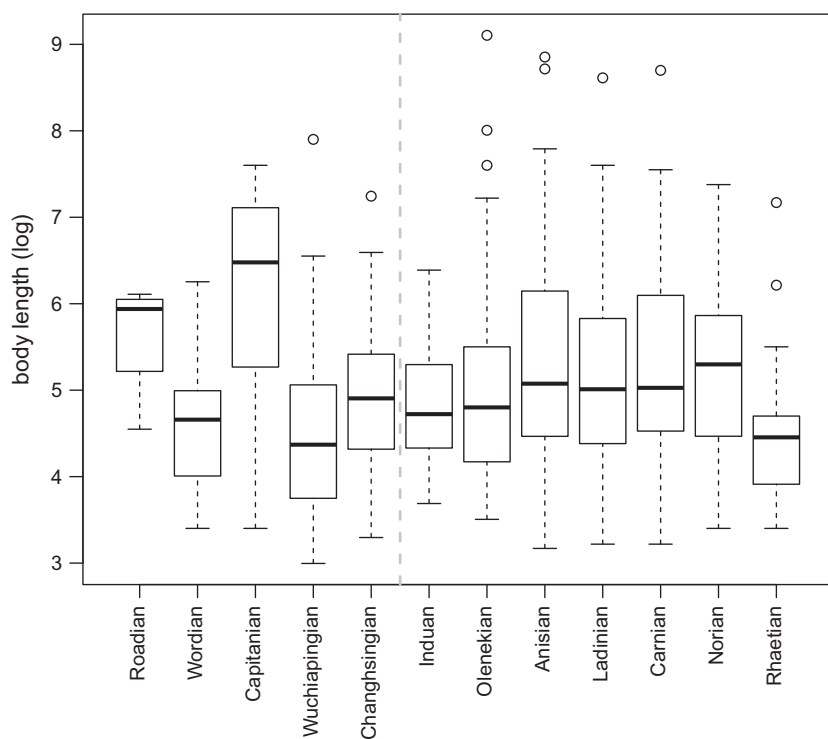
#### Patterns of diversity

High levels of phylogenetic clustering of extinction can disproportionately reduce diversity (Krug & Patzkowsky 2015) so the high phylogenetic signal in extinction in Actinopterygii could explain the huge fall in diversity seen in the Early Triassic (Fig. 2). The huge decline suffered by the ‘Palaeonisciformes’ was responsible for the decline in Actinopterygian diversity (Romano *et al.* 2014). Although not included in this study, the rise of Teleostei did not occur until some 20 myr after the PTME as indicated by their fossil record, from the Late Triassic through the Jurassic, and holosteans were still reasonably diverse into the Jurassic and Cretaceous (Friedman & Sallan 2012; Romano *et al.* 2014). The previous lack of evidence for a fall in fish diversity through the PTME may be because large groups, such as the ‘Palaeonisciformes’ were little studied (Friedman

& Sallan 2012; Sallan 2014) and sometimes omitted or undercounted. Many groups, including some crown groups (Hurley *et al.* 2007) did survive the PTME, and this eventually allowed for the rise to the huge diversity and disparity of today’s actinopterygians, including teleosts.

#### Patterns of body lengths through time

In the aftermath of mass extinctions, taxa are often reduced in size in a phenomenon known as the Lilliput Effect (Urbanek 1993). At the PTME, the reduction in size of surviving taxa has been attributed to selectivity against larger taxa (Song *et al.* 2011) or to poor environmental conditions reducing size within lineages (Rego *et al.* 2012). The exact nature of the Lilliput Effect has been debated (Harries & Knorr 2009) but our results



**FIG. 6.** Boxplots displaying the body lengths of species of non-teleostean Actinopterygii that become extinct through time. The body lengths of species that went extinct in each stage during the late Permian and Early Triassic following the PTME (dotted line) are shown. There is no evidence of a change in the sizes of taxa going extinct across the Permo-Triassic boundary.

support a model for the PTME that is not selective for body size. Therefore, any detected size decreases would arise from conditions in the post-extinction world (Rego *et al.* 2012). However, as we did not analyse within-lineage trends it is not possible to test between the alternative hypotheses of the Lilliput effect.

#### Body length selectivity

During the PTME, taxon loss appears to have been random with regard to body length (Table 2; Fig. 4). Similar results have been shown in phylogenetic analyses of different taxa during other mass extinctions (Smith & Jeffrey 1998; Friedman 2009; Harnik *et al.* 2014) including, importantly, actinopterygian fishes through the Cretaceous–Palaeogene mass extinction (Friedman 2009). Friedman (2009) found that body size was a significant selective factor before phylogenetic correction, but not after phylogenetic correction. Here we find that body size is a non-significant factor in mass extinction selectivity, both with and without phylogenetic correction.

Previous analyses have also noted that ‘dead clade walking’ taxa can have different patterns of body size or length compared to surviving species that prosper in later times (Romano *et al.* 2014; Sallan & Galimberti 2015). For example, selective differences in body length could be hidden by the presence of large-bodied ‘Palaeonisciformes’ that survived the PTME, only to succumb to extinction soon after (Romano *et al.* 2014). Here, we

tested this by marking lineages as extinct if they gave rise to fewer than ten descendant species in the post-extinction world. Even when this was done, there was no evidence for a selective signal in fish extinction, but there is some evidence here that both extremes of long and short body lengths are more susceptible to extinction (Fig. 5).

Our results are unexpected because extinction risk in a wide range of modern taxa is size-dependent (Gaston & Blackburn 1995; Olden *et al.* 2007). For example, larger body size in modern fish leads to higher rates of extinction in relation to climate change (Genner *et al.* 2010). However, this relationship is complex for modern fish (Olden *et al.* 2007). Another factor, larger population size, is related to higher survival probability in many taxa (O’Grady *et al.* 2004) but there is a weak inverse correlation between body size and population size in fish (Hutchings *et al.* 2012). Our results support analyses from the fossil record of fishes and other groups that generally show little evidence for selectivity by body length or size during mass extinctions (Friedman 2009; Tomiya 2013; Smits 2015). Furthermore, the modern signal for body size selectivity may be an artefact resulting from human impacts (Plotnick *et al.* 2016).

In agreement with Romano *et al.* (2014), we find little difference between body lengths of bony fishes in the late Permian and Early Triassic. However, we did not consider whether other biological or ecologically relevant traits might be selected during mass extinctions, such as palaeo-latitude and diet (Romano *et al.* 2014). Indeed, the increased phylogenetic signal across the PTME suggests



that other traits may have played a role in selectivity. For example, traits such as feeding modes (Smith & Jeffrey 1998; Friedman 2009) and geographic range size (Jablonski & Raup 1995; Harnik *et al.* 2014) are both associated with survival for taxa through different extinction events. We did not test for these in the current study because most taxa in our data set are known from single localities or single geological formations, and so reliable geographic and temporal ranges cannot be established. In the future, more clade-specific or biologically informative traits may provide evidence of selection acting on species' traits during mass extinctions, but there is no evidence for body length acting on selectivity during the PTME.

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## DATA ARCHIVING STATEMENT

All the trees, R code, and data used in this study are available on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.394hm>

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